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A Study of the Inheritance and Inter-relationships of some Agronomically Important Characters in Spring Barley

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Summary. The results of genetical analyses of data for the characters ear number, grain number per ear, 1000 corn weight and straw length are presented. These data were obtained from the F_1 and F_2 generations of a half diallel cross between 13 barley varieties, 4 of which were six-row types. Separate analyses were also conducted on the sub-set comprising two-row genotypes only.

Analyses of variance detected a high level of dominance in F_1 for all the characters and in general the dominance effects were directional and positive. Apparent overdominance resulting from interaction was detected in the F_1 of crosses between two-row and six-row parents for 1000 corn weight.

Evidence suggested that selection had resulted in the accumulation of dominant genes having an increasing effect on the morphological components of yield. A high proportion of dominant genes acting to increase straw length was also detected and it was concluded that considerable further shortening of the straw might be possible by selection in a segregating population though possibly at the expense of yield.

Genotypic correlation coefficients were computed and provided evidence that further genetic improvement for yield should be possible within the two-row genotypes.

Introduction

In breeding for increased yield in the small grain cereals, effective yield evaluation is not usually possible until the F_4 or F_5 generations. Selection in the early generations may consequently be mainly for the morphological components of yield such as the number of ears per plant, the grain number per ear and the weight per grain. Rasmusson and Cannell (1970) found that selection for yield components as a means of increasing total yield was very effective in certain situations. They could not however recommend it as a routine procedure because of the inconsistency of results. Yap and Harvey (1972) reported results of a genetic study on yield components in barley and concluded that selection for increased yield by direct selection for its components should be successful since these characters were controlled mainly by additive gene action and the three yield components were significantly correlated with grain yield. Adams (1967) has pointed out that since yield components are determined at different stages in the ontogeny of the plant they are affected differentially by environmental factors. Compensation between yield components may lead to negative correlations between them. This author stressed the need for continual investigation and analysis at the genetical, physiological and developmental levels, of yield components and their inter-relationships.

The results presented here were obtained from an experiment designed to provide genetical information on the control of a number of quantitatively inherited characters including components of yield and the production of diastatic enzymes. Thirteen parent varieties and their progeny were studied and results are presented for the characters ear number, grain number per ear, 1000 corn weight and straw length. A more detailed analysis of the yield component grain number per ear has already been published (Riggs and Hayter 1973) and a genetical study of time to ear emergence was described by Riggs and Hayter (1972).

Materials and Methods

The 13 spring barley varieties used are listed in Table 1 and details of their pedigrees and provenances were given by Riggs and Hayter (1972). Most of the two-row varieties were, at the inception of the experiment, of some commercial interest. The six-row varieties, with the exception of Scotch Bere (derived from an old Scottish land race), were chosen for their high diastatic enzyme activity during germination.

The material grown as Deba Abed (Riggs and Hayter 1972) was found not to be true to type and is referred to in this paper as "Stock 1".

Varieties were crossed according to the half diallel mating design and the parents F_1 and F_2 generations were grown together in two replicate blocks in the two seasons 1970 and 1971. Plants were randomized individually within each block at a spacing of 15 cms between rows and 7.5 cms between plants within rows. Each family was represented by 10 sibs in each block.

Ear number and straw length were recorded for each plant at harvest. The ears were then threshed and the grains counted and weighed. It was not found possible to obtain accurate direct measurements of yield per plant because unavoidable damage at harvest occasionally led to ear or grain loss.

Data were analysed according to the procedures appropriate to diallel mating designs and described by Mather and Jinks (1971). Analyses were conducted for the F_1 and F_2 generations of the 13×13 half diallel (13 HD) and for the 9×9 sub-set comprising two-row genotypes only (9 HD). For brevity the results from the 1971 season only are presented. The 1971 season was more favourable for growth than the 1970 season but the results were similar in both years.

In the analyses of variance for the 13 HD all items were tested against the average within - family variance for the F_1 and parents. This was very similar to the pooled block interaction mean square, Bt (Table 2). In the 9 HD all items were tested against the Bt item obtained from the analysis of the F_1 data.

Unweighted least square estimates for the genetic components D, H_1, H_2 and F (Mather, 1949) were obtained using statistics from pooled F_1 and F_2 data from both blocks. Using the terminology of Mather and Jinks (1971), these statistics were Vp, $\overline{Vr}$, $V\bar{r}$, $\overline{Wr}$, $\overline{Wr}_{12}$, $W\bar{r}_{12}$ and direct measures of E_0, E_1 and E_2, the within - family variances of the parents, F_1 and F_2 respectively.

Broad-sense heritability (h_B^2) and narrow-sense heritability (h_N^2) estimates were calculated from

$$h_B^2 = \frac{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{4}H_2 - \frac{1}{2}F}{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{4}H_2 - \frac{1}{2}F + E} \quad \text{and}$$

$$h_N^2 = \frac{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{2}H_2 - \frac{1}{2}F}{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{4}H_2 - \frac{1}{2}F + E}$$

To obtain genotypic correlations the variances and covariances between the three yield components, straw length and time to heading were partitioned into the average within-family and the between-family components. For this purpose data from the two blocks were pooled.

Results

The mean values of the four characters for each parent variety are shown in Table 1. The six-row varieties produced fewer ears and had longer straw than the two-row varieties. They also exhibited relatively low corn weights. The closely related two-row parents Midas and Golden Promise had particularly short straw and low corn weights.

Diallel Analysis

For each array, Vr, the variance of all offspring of the rth parent, and Wr, the covariance between the offspring and the non-recurrent parent, were calculated (Jinks 1954). The relationship between Wr and Vr provides tests of the genetic model assumed. Heterogeneity of Wr-Vr over arrays indicates non-allelic interaction and the failure of the additive-dominance model to fit the data. In the absence of interaction, heterogeneity of Wr + Vr indicates variance amongst arrays for dominance effects.

For the character ear number no non-allelic interaction was detected by this test in either the 13 HD or the 9 HD. Tables 2 and 3 show that both additive and non-additive genetic variance was detected in the F_1 generation but that by F_2 in the 13 HD only additive genetic variance was present. In the 9 HD F_2 no genetic variance at all could be detected. The estimated genetic components for this character (Tables 4 and 5) indicated only additive variance in the 13 HD whereas in the 9 HD only the dominance components were significant. No estimates of heritability could therefore be made in either case. Although directional dominance was indicated by the analyses of variance for both diallel groups, the correlation of Yr, the parent mean, and Wr + Vr reached significance only in the 9 HD F_1. Since Wr + Vr is an inverse measure of dominance the negative sign of the correlation coefficient shows that dominant genes determined high ear number. It is apparent that the different analyses lead to somewhat conflicting conclusions and it seems likely that the genetic effects were obscured by environmentally conditioned fluctuations in the expression of the character.

The results of the analyses for grain number per ear have been described in a previous publication (Riggs and Hayter 1973) and are summarized here.

Considerable additive and non-additive genetic variance was detected in the 13 HD, and in the 9 HD non-additive variance was attributable almost entirely to the b_1 item, the mean grain number per ear for the hybrids exceeding that for the mid-parents by 7.4%.

The H_1 and H_2 components were large for the 13 HD (Table 4) but non-allelic interaction was detected in the 9 HD and the genetic components were not estimated. The high level of dominance detected in the 13 HD was no doubt due to the allele V which determines two-row expression and is dominant to the allele v, determining six-row expression, at a single locus on chromosome 2. The gene asymmetry detected (i.e. $H_2/4H_1 < 0.25$) was probably due to the unequal numbers of two-row and six-row genotypes. The ratio $\frac{1}{2}F/\sqrt{D(H_1 - H_2)}$ was close to 1 showing that additive and dominance effects were in approximately the same proportion over all loci, and the ratio $(4DH_1)^{\frac{1}{2}} + F/(4DH_1)^{\frac{1}{2}} - F$ showed that the proportion of dominant to recessive genes or effective factors was approximately 2.6 to 1. Both broad and narrow-sense heritability estimates were high.

For 1000 corn weight considerable non-allelic interaction was detected in the 13 HD and the slope of the re-

Table 1. Mean measurements for four characters in thirteen barley varieties

	ear number	grain no. per ear	1000 corn weight (g)	straw length (cm)
1. Olli*	3.00	38.65	38.21	97.5
2. Pirkka*	2.41	42.89	36.73	95.0
3. Cambrinus	4.40	19.82	45.32	79.8
4. Ymer	4.95	19.95	43.09	81.9
5. Stock 1	4.05	23.30	43.16	90.4
6. Scotch Bere*	3.05	41.35	40.12	107.3
7. O.A.C. 21*	2.43	39.47	35.95	111.9
8. Golden Promise	3.85	20.90	34.43	65.8
9. Maris Baldric	3.85	20.20	44.61	80.4
10. Midas	3.10	22.85	35.51	69.1
11. Mosane	3.70	19.70	41.95	84.7
12. Sultan	4.25	19.55	42.12	80.3
13. Boreham Warrior	3.85	22.37	50.47	81.6
	±0.339	± 1.423	± 1.393	± 3.218

* six-row

Table 2. Analyses of variance of a 13 × 13 diallel table (13HD) for four characters

		ear number		grain no. per ear		1000 corn weight		straw length	
Item	d.f.	F_1 MS	F_2 MS	F_1 MS	F_2 MS	F_1 MS	F_2 MS	F_1 MS	F_2 MS
a (additivity)	12	55.00'''	32.22'''	3606.7'''	5046.4'''	1653.1'''	1509.1'''	14031.9'''	12385.2'''
b (dominance)	(78)	5.83'''	2.96	346.4'''	144.1'''	838.1'''	217.2'''	843.8'''	299.8'''
b_1 (direction)	1	109.97'''	3.88	1807.6'''	100.4	16699.3'''	3017.2'''	22795.2'''	5571.2'''
b_2 (distribution)	12	3.26	3.99	632.6'''	223.7'''	664.1'''	310.1'''	354.5''	69.7
b_3 (specificity)	65	4.70'''	2.75	271.1'''	130.1'''	626.2'''	157.0'''	596.4'''	261.2'''
Blocks	1	6.98	12.86'	2090.5'''	1558.0'''	1215.7'''	91.3	706.4''	92.6
Pooled block interactions (Bt)	90	2.54	3.02	40.5	108.9'''	31.9	88.8'''	124.2	152.8''
Within-family variance (F_1 + parents)		2.53 (1631 d.f.)		34.2 (1608 d.f.)		41.1 (1620 d.f.)		102.0 (1620 d.f.)	

All items tested against the appropriate within-family variance.
', '', ''', significant at P = 0.05, 0.01 and 0.001 respectively.

Table 3. Analyses of variance of a 9 × 9 diallel table (9HD) for four characters

		ear number		grain no. per ear		1000 corn weight		straw length	
Item	d.f.	F_1 MS	F_2 MS	F_1 MS	F_2 MS	F_1 MS	F_2 MS	F_1 MS	F_2 MS
a (additivity)	8	1.06''	0.56	12.10'''	7.63'''	89.08'''	107.89'''	150.48''	214.54'''
b (dominance)	(36)	0.96'''	0.35	2.69''	1.98	21.31'''	10.39'''	35.89'''	21.47''
b_1 (direction)	1	10.47'''	0.08	33.60'''	26.00'''	381.29'''	127.35'''	669.94'''	255.19'''
b_2 (distribution)	8	0.27	0.54	1.18	1.89	9.73''	7.17'	20.04'	11.04
b_3 (specificity)	27	0.81''	0.30	1.99'	1.11	11.41'''	7.01''	17.11'	15.90'
Blocks	1	0.09	0.40	29.19'''	11.33'	91.04'''	20.80'	10.68	23.92
Pooled block interactions (Bt)	44	0.32	0.40	1.03	1.57	3.21	5.37	8.79	12.86

All items tested against the appropriate Bt from the F_1 analysis.
', '', ''', significant at P = 0.05, 0.01 and 0.001 respectively.

Table 4. Components of variation for three characters. Data from 13HD F_1 and F_2

	ear number	grain no. per ear	straw length
D	0.399 ± 0.07	91.463 ± 4.29	176.09 ± 5.5
H_1	0.404 ± 0.33	77.865 ± 19.95	138.06 ± 25.4
H_2	0.306 ± 0.29	47.884 ± 17.62	120.82 ± 22.4
F	-0.195 ± 0.24	74.264 ± 14.37	13.48 ± 18.3
$(H_1/D)^{\frac{1}{2}}$	-$^{+}$	0.92	0.89
$H_2/4H_1$	-	0.15	0.22
$\frac{1}{2}F/\sqrt{\{D(H_1-H_2)\}}$	-	0.71	-
$(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F$	-	2.57	-
h^2_B	-	0.91	0.92
h^2_N	-	0.60	0.69
$r(Yr, Wr+Vr)F_1$	0.29 n.s.	0.90***	-0.95***
$r(Yr, Wr+Vr)F_2$	-0.40 n.s.	0.82***	-0.86***

+ ratios were not computed where the components failed to reach significance.

Table 5. Components of variation for three characters. Data from 9HD F_1 and F_2

	ear number	1000 corn weight	straw length
D	0.056 ± 0.07	21.877 ± 1.53	54.181 ± 3.51
H_1	0.818 ± 0.33	27.538 ± 7.06	47.032 ± 16.18
H_2	0.784 ± 0.29	24.387 ± 6.22	40.301 ± 14.24
F	-0.054 ± 0.23	10.165 ± 5.05	40.545 ± 11.57
$(H_1/D)^{\frac{1}{2}}$	-$^{+}$	1.12	0.93
$H_2/4H_1$	0.24	0.22	0.21
$\frac{1}{2}F/\sqrt{\{D(H_1-H_2)\}}$	-	0.61	1.06
$(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F$	-	1.52	2.34
h^2_B	-	0.78	0.70
h^2_N	-	0.43	0.35
$r(Yr, Wr+Vr)F_1$	-0.77*	-0.93***	-0.90**
$r(Yr, Wr+Vr)F_2$	-0.21 n.s.	-0.69*	-0.89**

+ see footnote to table 4.

gression of Wr on Vr was considerably less than 1 (Fig.1). The six-row genotypes, with the exception of the Scotch Bere array, displayed an excess of recessive genes. The apparent overdominance indicated by the intercept of the regression on the Wr axis (Jinks 1954) was reflected also in the extremely large b_1 item in the analysis of variance (Table 2).

When analyses were conducted on the 9HD no non-allelic interaction was detected in the analysis of Wr-Vr.

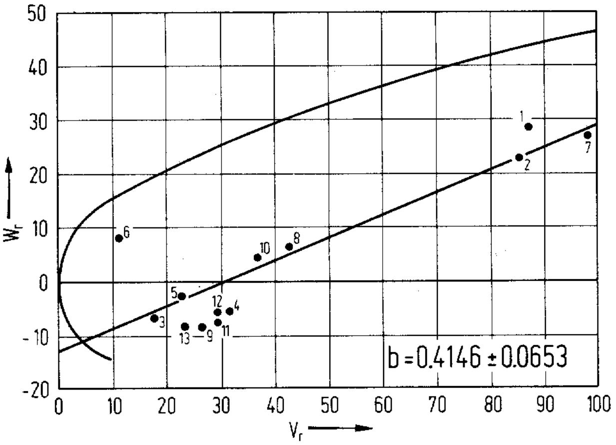

Fig.1. Wr, Vr regression for 1000 corn weight, 13HDF_1

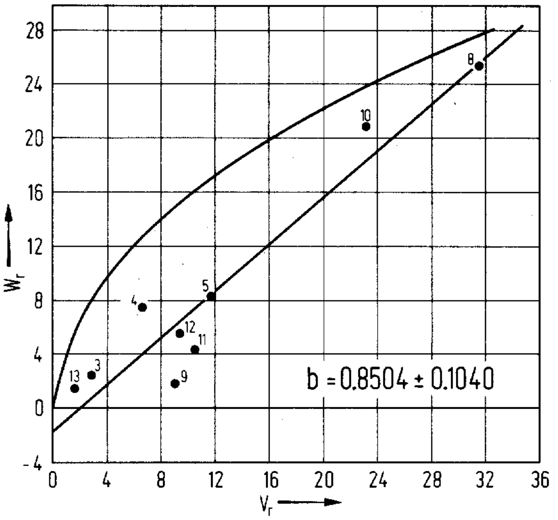

Fig.2. Wr, Vr regression for 1000 corn weight, 9HDF_1

The ratio $(H_1/D)^{\frac{1}{2}}$ was approximately 1, indicating complete dominance, and gene symmetry was almost complete. The Wr, Vr regression gave a slope not significantly different from 1 (Fig.2) and the positions of the points on the line show that the Golden Promise and Midas arrays contained mostly recessive genes whereas the arrays of the other seven varieties contained mostly dominant genes. The correlations between Yr, the parent means, and Wr + Vr clearly demonstrate (Table 5) that high 1000 corn weight was determined by dominant genes. The apparent overdominance detected in the 13HD F_1, was clearly the result of non-allelic interaction in crosses between two-row and six-row parents.

In the 9HD the ratio of additive to dominance effects was not entirely constant over loci and there were on average approximately 1.5 dominance genes or effective factors for each recessive factor involved in the control of this character.

Considering finally the character straw length, additive and dominance effects were found to be operating in the control of this character and in both the 13HD and the 9HD dominance was almost complete. In the 9HD the dominance was attributable almost entirely to the b_1 item in the analysis of variance and the mean height of the hybrids exceeded the mid-parent height by 8.8%.

The level of dominance was constant over all loci in the 9HD and there were approximately 2.3 dominance genes or gene groups for each recessive gene or gene group operating. Broad-sense heritabilities were high in both diallel groups but the narrow-sense heritability estimated for the 9HD was relatively low.

Genotypic Correlations

Table 6 shows the genotypic correlation coefficients computed from parents and F_1 data for pairs of characters, including time to ear emergence. Levels of significance have been assigned as if the correlation coefficients were phenotypic i.e. with n-2 degrees of freedom. The genotypic and phenotypic correlation coefficients were very similar and this procedure is unlikely to lead to erroneous conclusions.

Similar correlations in both the 9HD and the 13HD were found between the character straw length and the characters grain number per ear, 1000 corn weight and time to ear emergence. Thus long straw was associated with early heading, high 1000 corn weight and high grain number.

In the 9HD long straw was strongly associated with high ear number but there was a weak negative association between ear number and time to ear emergence. This latter result supports the results of Hayes (1965) from a diallel between 10 two-row parents, that the early genotypes tended to produce more ears per plant. On the other hand, Grafius (1959), working with six-row barley, showed that earliness tended to prevent full expression of the potential tillering capacity of the genotype.

Positive correlations were detected in the 9HD between time to ear emergence and grain number per ear but time to ear emergence was of little or no significance in the expression of the yield component 1000 corn weight. Ear number and grain number per ear were not correlat-

Table 6. Genotypic correlations between pairs of characters

13 HDF$_1$, n = 91 and 9 HDF$_1$ (below), n = 45		EN	GPE	TCW	SL
ear number	(EN)				
grains per ear	(GPE)	- 0.49*** (0.12)			
1000 corn weight	(TCW)	0.05 (0.47***)	- 0.59*** (0.49***)		
straw length	(SL)	- 0.47*** (0.58***)	0.36*** (0.32*)	0.37*** (0.72***)	
time to ear emergence	(EE)	0.49*** (-0.26*)	- 0.30** (0.67***)	- 0.22* (0.12)	-0.62*** (-0.30*)

ed though each was positively correlated with 1000 corn weight.

In the 13 HD the signs of some of the correlations were the reverse of those in the 9 HD. These rather striking reversals can only be explained in terms of the presence in the 13 HD of the six-row genotypes which were generally taller and earlier than the two-row genotypes and which had fewer ears, higher grain number per ear and lower 1000 corn weight. Progeny of crosses between two-row and six-row parents will carry dominant genes for long straw, early heading and two-row head type. They will also exhibit non-allelic interaction conditioning high 1000 corn weight.

Discussion

The results must be regarded as applying specifically to the varieties used in the study but these varieties represent a fairly diverse sample of material selected by barley breeders in Denmark, Finland, Sweden, Belgium, Holland, England and Canada. Thus the genetical architectures of the characters measured and their inter-relationships provide an insight into the direction taken by artificial selection.

Immediately apparent from the genetical analyses is the high level of dominance detected in the inheritance of all the characters. Thus the heterosis for yield detected by other workers cannot necessarily be explained (Williams 1959) as simply the result of multiplicative interaction between components which are determined by essentially additive genetic systems.

The genetical analyses on the character ear number were to some extent obscured by unaccounted variability resulting from environmental effects. Within-family variances in crosses between six-row parents were found to be lower than those in the two-row group indicating genotype-environment interaction. Thus the two-row genotypes exhibited a greater capacity to respond to environmental fluctuations by tillering to a greater or lesser extent. This was noted also by Johnson and Aksel (1959). It is possible that in our experiment the complete randomization of plants of different genotypes might have led to fluctuations in tillering as a response to inter-plant competition even though the plants were equally spaced.

The correlation of Yr and Wr + Vr showed that dominance in the F$_1$ increased 1000 corn weight in the 9 HD and straw length in both diallel groups. Dominance increased ear number in the two-row genotypes. Grain number per ear in the 13 HD was apparently influenced mainly by the Vv locus, with the two-row genotype dominant. The analysis of variance in the 9 HD indicated directional dominance in both F$_1$ and F$_2$ but because of non-allelic interaction the Wr, Vr analysis could not be used to determine the direction of dominance.

Dominance acted in general towards higher expression of the main components of yield and selection has clearly resulted in a preponderance of dominant genes controlling these characters. This is indicated by the large positive values of F in Tables 4 and 5. Mather (1973) argued that directional selection for a character would be expected to result in dominance and duplicate type interaction both acting in the direction favoured by selection. Genes determining a character which is under stabilizing selection would be expected to show weaker dominance of an ambidirectional kind and interaction either absent or weak and ambidirectional. Such a situation was reported by Riggs and Hayter (1972) for the time to ear emergence in barley, a character which would have been under stabilizing selection.

Dominant genes were also preponderant in the control of straw length, yet selection pressure would nowadays be towards shorter straw, against the direction of dominance. However, for much of the period of cultivation of the crop, competitiveness against weeds would have favoured greater height, and the value of the straw might have led to some selection for increased height. Selection towards fixation of the recessive alleles in all of a number of genes would be somewhat hampered by the relative infrequency in a segregating population of such genotypes but considerable further shortening of the straw should be possible. The positive correlations of straw length with grain number per ear and 1000 corn weight suggest, however, that this might be done at the expense of yield. Indeed the preponderance of dominant genes for long straw might well be the result of a correlated response to selection for yield.

In the analyses of variance for the F_1 generation, the b_2 item reached significance for all the characters except ear number in both diallel groups and for grain number per ear in the 9 HD. This item indicates that some parents contained more dominant alleles than others. In the 9 HD the b_2 item was significant for the character s 1000 corn weight and straw length. This was probably due to the presence of Midas and Golden Promise which contrast strongly with the other varieties in the two-row group in their expression of these characters (Table 1). They combine agriculturally desirable short straw with undesirably low corn weights and both arrays exhibited an excess of recessive alleles determining these characters. Indeed, both varietes carry a major recessive gene for shortness.

The spacing between plants used in this experiment is probably fairly typical of that used by many barley breeders for single F_2 plant selection. The heritability estimates obtained are therefore of some interest. Considering the estimates of h^2_N from the two-row material, the effectiveness of selection is expected to be fairly high for 1000 corn weight, less so for straw length and uncertain for ear number and grain number per ear.

The interaction detected in crosses between two-row and six-row parents for the character 1000 corn weight may well be a fairly general phenomenon. Indeed we have obtained similar results with different sets of parents though the phenomenon was apparently not observed by Hayes and Khalifa (1974) who also used two-row and six-row parents in a diallel experiment. The high level of heterosis in such crosses (18 % in this material) might be of some significance in the production of commercial F_1 varieties provided that small lateral grains were not produced.

The genotypic correlations observed in this material could have been the result of linkage, pleiotropy or gene association without linkage. They could also be the result of environmentally induced compensations between the characters which are only indirectly the result of gene action. Furthermore the correlations found in the parents and F_1 generations are arguably not as meaningful to the breeder as the relationships found between characters in homozygous lines. The correlations between components in the hybrids will depend upon the relative proportions of additive and non-additive gene action in the expression of the individual characters and may well change with increasing homozygosity.

In the two-row material studied here the positive correlations between yield components are probably the result of positive selection in the breeding of the parents for high expression of these components. We have seen that high expression is generally determined by dominant genes and these will have become associated or linked in coupling.

Rasmusson and Cannell (1970) computed phenotypic correlations between yield and the morphological components in two populations at F_4 and again, the following season, at F_5. The correlations were very different in the two generations and the authors argued that these results supported the view of Adams (1967) that control of component relationships is largely environmental. Under conditions of intense inter-plant competition compensatory variation between components may lead to negative associations (Adams 1967). The positive correlations found in these data presumably indicate that such compensation was not a general phenomenon under the conditions of trial and that environmental stress was absent. It would appear that further genetic improvement for yield in this gene pool should be possible. Indeed the fact that component compensation may occur means that negative correlations would not necessarily indicate limitations to the improvement of yield.

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